HISTOLOGICAL STUDIES ON THE DIGESTIVE SYSTEM OF A STARFISH, HENRICIA, WITH NOTES ON TIEDEMANN'S POUCHES IN STARFISHES [1]

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In starfishes of the genus *Henricia* (Family Echinasteridae), the digestive tract is a complex system presenting many highly specialized features and contrasting markedly with the much simpler digestive organs of forms such as *Asterias* or *Pisaster*. In consequence of a number of descriptive and experimental studies, structural and functional aspects of feeding and digestion in Asteriidae are reasonably well understood; in contrast, very little is known of the details of structure and function in the alimentary tract of *Henricia*. From the functional standpoint, for instance, we remain in ignorance of the normal food of *Henricia* (Mortensen, 1927, p. 120), and of its mode of feeding. Anatomy and histology have received somewhat more attention: Cuénot (1887) devotes some descriptive remarks to the digestive system in *Cribella oculata* (= *Henricia sanguinolenta*), and Hayashi (1935) includes sections on the structure and histology of the digestive tract in his article on the anatomy of a Japanese variety of *H. sanguinolenta* which later (1940) he considers a separate species, *H. ohshimai*. Hayashi's account is reasonably accurate as far as it goes, but in terms of the digestive tract it is disappointingly superficial, omitting to mention several conspicuous features and relationships that are both interesting and significant. The present study was undertaken originally as a necessary foundation for contemplated experimental studies on the digestive tract. It presents a more nearly complete description of anatomical and histological details, seeks to combine these with histochemical characteristics of parts of the digestive system as possible clues to function, and draws attention to unique features of the system unaccountably omitted from previous descriptions.

Prominent among these are the structures associated with the pyloric caeca which Ludwig and Hamann (1899) named "Tiedemann's pouches" in recognition of their discoverer. In his epochal monograph of 1816, which laid the foundations of our modern knowledge of echinoderm morphology, Friedrich Tiedemann briefly described a detail of structure in *Astropecten auranciacus,* as follows (p. 48): "On the lower surface of each caecum there is a small, elongate, and hollow appendage, which commonly contains a yellowish fluid. Perhaps this appendage is a kind of secretory organ." Cuénot (1887) called attention to the singular development of these structures in starfishes of the families Asterinidae and Echinasteridae (p. 34): ". . . the median sac is considerably elongated and forms a voluminous reservoir, which, in the natural position of the animal, is situated below the radial caecum; this reservoir runs about half or three-quarters the

length of the caecum and is marked by regularly spaced oblique folds; it opens widely into the gastric sac, of which it is nothing more than a continuation." (See also Cuénot's Plate II, Figures 11 and 18.)

Considering the conspicuous and distinctive nature of these structures in the starfishes that possess them, it is surprising that Tiedemann's pouches (or Tiedemann's diverticula, as they are also called) have attracted so little attention with regard to either structural details or functional possibilities. Vogt and Yung (1888), referring to the relatively small pouches in *Astropecten,* mention that solid food has been observed in the pouches but not in the pyloric caeca themselves. Irving (1924), in his discussion of ciliary currents in *Patiria miniata,* describes Tiedemann's pouches as the median ducts of the caeca which bear the glandular pockets on their aboral walls. Misled by this description, I later (Anderson, 1953) used the same terminology in discussing the pyloric caeca of *Asterias forbesi.* It must be noted that the caeca of the family Asteriidae do not possess Tiedemann's pouches and that where they do occur, these pouches are not the median ducts themselves but form extensive appendages on the oral sides of the median ducts. Finally, Hayashi (1935) pays practically no attention to these conspicuous structures in his anatomical study of *Henricia,* saying only (p. 9), "Each caecum has a spacious median canal which is elongated dorso-ventrally in cross-section, and the wall is thin and folded."

We thus appear to lack altogether any detailed information on structure and function in Tiedemann's pouches. Accordingly, in the present study some emphasis is placed upon the anatomical and histological features of Tiedemann's pouches in *Henricia,* and upon the very considerable differences that exist between the pouches in *Henricia* and those in *Patiria,* a member of the other family (Asterinidae) in which such pouches typically occur, according to Cuénot (1887). Where pertinent, brief remarks are included concerning preliminary studies of the pouches in *Asterina gibbosa, Astropecten irregularis* and *armata,* and *Linckia guildingi.*

Materials and Methods

Small to moderate-sized specimens of *Henricia leviuscula* were collected beneath stones in the intertidal zone at Point Piños, Pacific Grove, Calif. They were maintained in running sea-water in one-gallon jars provided with escape-proof collars of plastic screening. The specimens could not be induced to feed upon any of the variety of items readily accepted by *Patiria* and other species, but as they remained in apparently vigorous condition for periods of two months or more,

the possibility exists that they were feeding unobserved upon suspended particulate material in the water, or upon the algal and bacterial film on the walls of their containers. Comparative and confirmatory observations were made at Woods Hole on locally-collected specimens of *Henricia sanguinolenta* maintained under similar conditions. It is apparent that the two species do not differ significantly in the details of their internal anatomy, and the results to be reported are composite.

Gross anatomical studies involved specimens dissected after treatment with $MgCl_2$ (8% in tap water) to prevent movement or autotomy. For histological examination, tissues were fixed in Helly's fluid, washed, dehydrated, imbedded in paraffin, and sectioned serially at 7 to 10 μ; or fixed in Baker's formol-saline, post-chromed 24 hours in potassium bichromate, imbedded in gelatin, and sectioned on the freezing microtome. Tissues that included parts of the body wall were decalcified by soaking for approximately a week in 5% aqueous disodium ethylene-dinitrilo-tetraacetate (EDTA), a chelating agent, between fixation and dehydration steps.

For general study and orientation, paraffin sections were stained with Harris' hematoxylin and eosin. For the demonstration of muscle fibers, connective tissue, cell membranes, flagella and their basal bodies, and secretion granules, excellent results were obtained by the use of Mallory's phosphotungstic acid hematoxylin. Glycogen and other polysaccharide compounds were demonstrated by a periodic-acid-Schiff technic, controlled by salivary digestion, and meta-chromatic substances were stained by overnight exposure to very dilute solutions of toluidine blue. Steedman's Alcian Blue technic, as given by Pearse (1953), was employed for staining acid mucopolysaccharides. The frozen sections of gelatin-imbedded material were colored with Sudan black, counterstained with carmalum, to reveal lipid deposits.

Observations

A. Anatomy

As in starfishes generally, the digestive tract of *Henricia* is essentially a tube, running from mouth to anus in the short vertical axis of the body, divided into specialized successive regions termed cardiac stomach, pyloric stomach, and intestine (esophagus and rectum are additionally distinguished by many authors). The pyloric stomach gives off a pair of glandular appendages, the pyloric caeca, into each ray, and the intestine (or rectum) bears an exceptionally well-developed group of sacculate appendages, of unknown function, termed rectal caeca or intestinal caeca.

Viewed from below, as in Figure 1, the mouth appears as a stellate opening bounded by 5 peristomial lobes which approach each other centrally. When the animal is undisturbed, the mouth is usually partially open, as in this photograph. Hayashi (1935) terms the cardiac stomach, into which the mouth opens. "rudimental." It is relatively small, compared with that of *Asterias*, for example, and lies wholly within the circular frame bounded by the proximal ambulacral ossicles (Fig. 2). The stomach consists largely of a series of structures termed "esophageal pouches" by Cuénot (1887). There are 10 of these, 5 radial and 5 interradial in position; each radial pouch lies just medial to the large proximal ambulacral ossicle in its ray and is movably bound to this ossicle by a pair of

Figures 1 through 27 illustrate features of the digestive system in *Henricia;* Figures 28 through 31 show details of Tiedemann's pouches in *Patiria miniata.*

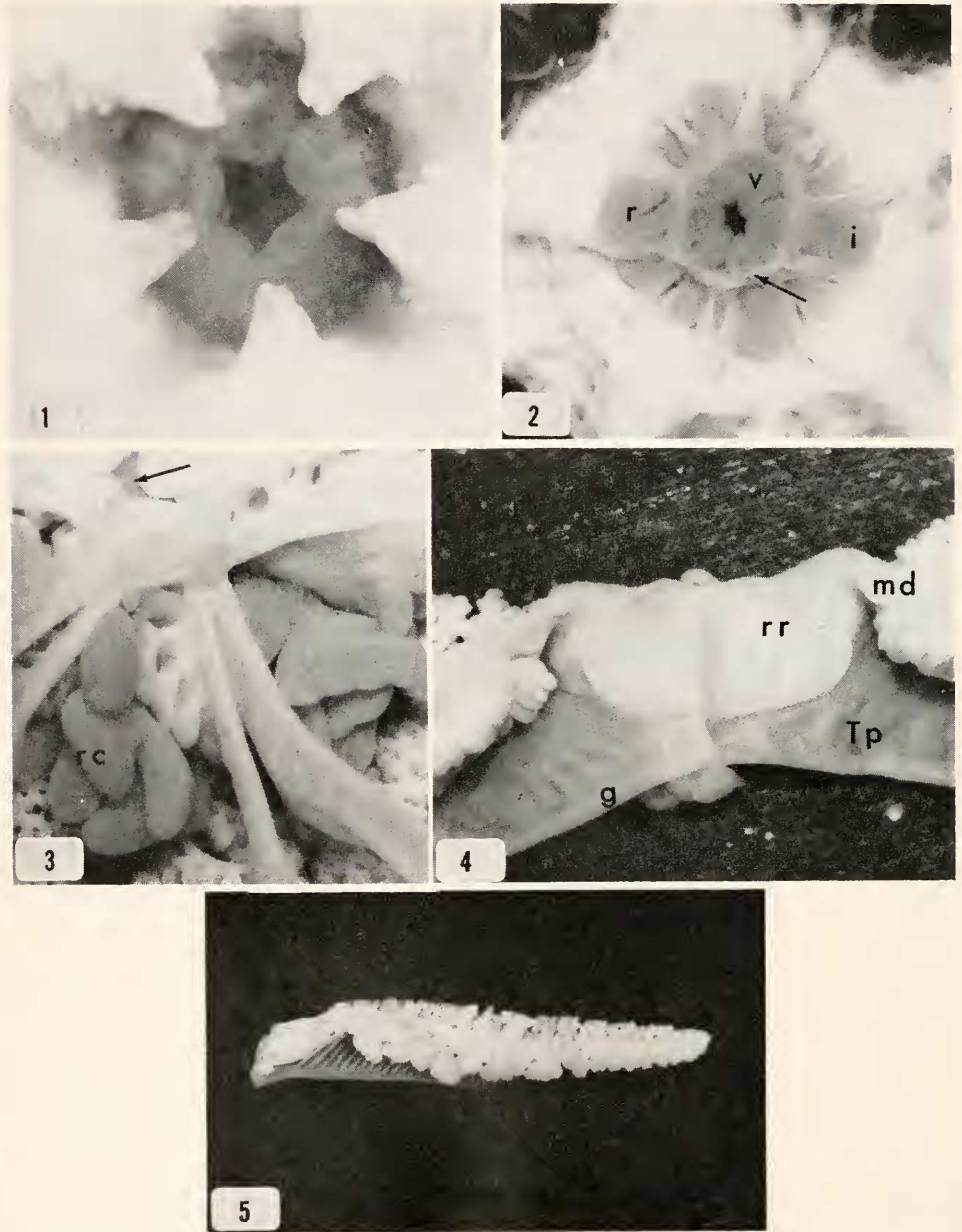FIGURE 1. Oral view of living specimen, showing partially open mouth surrounded by peristomial membrane. Approximately 20 ×.

FIGURE 2. Cardiac stomach from above, after removal of all aboral parts by transecting the pyloric stomach at the line indicated by the arrow. Note radial pouches (*r*); interradial

stout, fibrous retractor strands.   From the same origins a pair of longer strands pass upward to insertions higher on the wall of the stomach.   Hayashi remarks on the thick and compact appearance of these retractor strands in contrast to the highly branched fibers in *Asterias;* in *Henricia,* although short strands do extend to the outer surface of the adjacent esophageal pouches, these are neither so numerous nor so extensive as those forming what has been termed the intrinsic retractor mechanism in *Asterias* and *Patiria* (Anderson, 1954, 1959).

Above the interradial pouches the wall of the stomach folds inward longitudinally to form 5 or 6 (usually 5) large, centrally-directed bulges that almost occlude the lumen of the stomach but leave a narrow, stellate central passageway (Fig. 2). These swollen vesicles are separated from one another by deep, radiating folds which are restricted lateral extensions from the angles of the central passage and which, in consequence of their radial positions, form conspicuous gutters leading upward from the cavities of the radial esophageal pouches.   Above the level of these alternating vesicles and gutters the stomach is encircled by a slender fibrous girdle, into which the longer retractor strands from each ray insert.   There is no real constriction marking the separation between cardiac and pyloric portions of the stomach, and in the absence of other landmarks the regions above this circumferential girdle will be considered as belonging to the pyloric stomach. This is in agreement with the situation in *Patiria,* where a similar fibrous girdle has been taken to mark the upper limit of the cardiac stomach (Anderson, 1959).

Just above the level of the girdle, the pyloric stomach tapers somewhat, and its walls are perforated by a marginal opening at each of its radial angles. Each of these 5 openings leads into a duct which immediately bifurcates, giving rise to pale, translucent, cylindrical branches forming the tubular proximal channels that expand vertically into the two Tiedemann's pouches in its ray (Figs. 3, 4, 5). It should be noted that each marginal passage constitutes, in effect, a continuation of one of the radial gutters leading upward between the vesicles of the cardiac stomach, from a radial esophageal pouch.

Above the marginal openings, the pyloric stomach forms 10 radiating branches, rather deep in the vertical dimension, two leading towards each ray.   In each of these branches the side walls evaginate and are thrown into coarse folds, forming what I shall call radial reservoirs, with creamy-white, opaque walls.   The radial reservoir tapers upward and outward, narrowing as the underlying Tiedemann's pouch expands, and becomes the median duct of one of the paired pyloric caeca

pouches (i) ; vesicles (v) surrounding the central aperture; and the stout retractor harness sending strands over the radial pouches to attach on the circumferential girdle (*arrow*) marking the boundary between cardiac and pyloric stomach.   Approximately 15 ×.

FIGURE 3.   Aboral parts of the digestive system viewed from below.   Arrow indicates the central lumen of the pyloric stomach, from which the caecum-pouch complexes radiate in pairs (for details of these parts, see following figures).   Note the well-developed rectal caeca (*rc*). Approximately 15 ×.

FIGURE 4.   Basal parts of one pair of caecum-pouch complexes, cut off from central attachments and spread apart to show components.   Tiedemann's duct widens into Tiedemann's pouch (*Tp*), with gutter (*g*) forming its oral margin; above, the median duct (*md*) of the caecum widens into the thick-walled radial reservoir (*rr*) by which it connects to the pyloric stomach. Approximately 15 ×.

FIGURE 5.   A single caecum-pouch complex, cut off at left from its attachment to the pyloric stomach, showing relationship between Tiedemann's pouch (note parallel channels traversing its walls), radial reservoir, median duct, and lateral diverticula.   Approximately 5 ×.
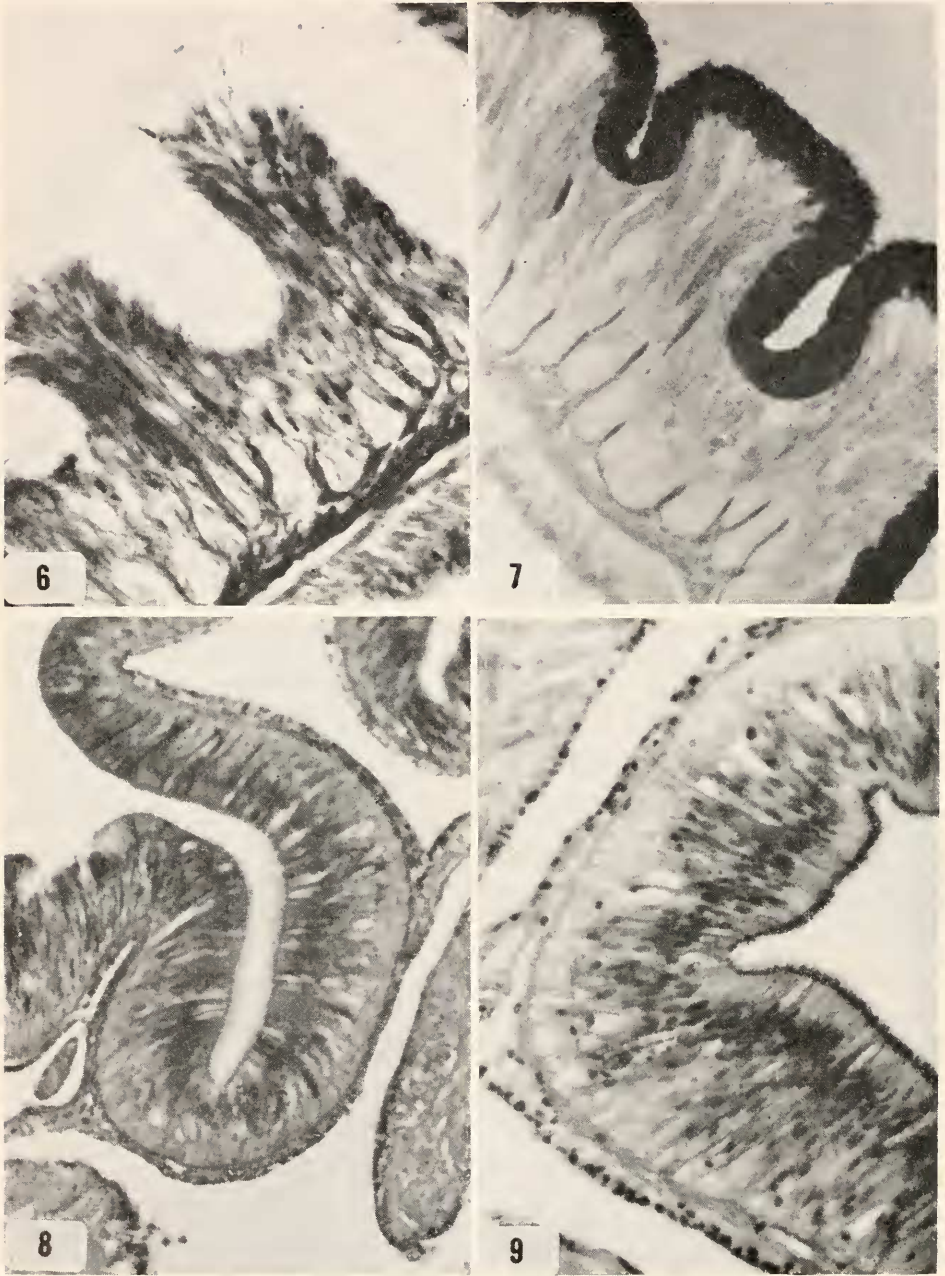
FIGURE 6. Extreme lower end of cardiac stomach ("esophagus"); note the heavy partitions extending upward from the connective-tissue layer; the tall epithelial cells with apparently empty distal ends; and the strands of secretory granules marking locations of the few zymogen cells in this area. Phosphotungstic acid hematoxylin; 470 ×.

(Figs. 4, 5). The first of the lateral diverticula of the pyloric caecum leaves the median duct somewhat beyond the end of the radial reservoir.

The figures clearly demonstrate that the pyloric caecum-Tiedemann pouch complex is dual in nature. The aboral part, consisting of the median duct with its many lateral diverticula, has its affinities with the radial reservoir, of which it appears to be a continuation. Tiedemann's pouch, on the other hand, altogether different in gross appearance, originates almost at the junction between cardiac and pyloric portions of the stomach and is evidently closely related to the lower region. The two ducts, the median duct and what we may call Tiedemann's duct, accompany each other and are closely bound together, but their cavities are completely separated by a continuous partition. Passing outward, the lower duct becomes a gutter that forms the oral margin of the deep, narrow pouch, and the body of the pouch itself extends between this gutter and the median duct of the pyloric caecum above. Throughout its length, the side walls of the pouch are traversed by a series of diagonal, parallel lines, giving the external appearance of the "regularly-spaced oblique folds" remarked by Cuénot (1887). Proceeding outward, the depth of the pouch decreases gradually, and at its outer end (about two-thirds the length of the caecum from its base) the oral gutter enters the floor of the median duct of the caecum (Fig. 5).

The roof of the pyloric stomach shows folds corresponding to the radial branches of the walls; these converge centrally upon the opening of the intestine. I can add nothing to Hayashi's description of the anatomy of this portion of the digestive tract, or of the rectal caeca which are extraordinarily well developed in *Henricia* (Fig. 3).

B. Histology

Histologically, the gut wall of *Henricia* presents the general features that appear to be standard throughout the Asteroidea. The usual tissue layers are present—peritoneum, muscular layers, connective-tissue layer, nerve plexus layer, and lining epithelium—and occupy the same relative positions as in other starfishes. The chief inadequacies of Hayashi's otherwise good account describing these layers involve his omission of significant details concerning the lining epithelium. This is basically a very tall layer, composed of what may be termed "typical" cells—long, slender cells, crowded together, with their ovoid nuclei lying at varying levels in the epithelium; each cell is provided, usually, with a single flagellum, springing from an apical basal body that sends a tapering fibril downward towards the nucleus. Better developed in some parts of the stomach than in others, longitudinal supporting fibrils also run through the basal portions of the

FIGURE 7. Adjacent section, showing intense metachromatic staining with toluidine blue in the distal areas that do not stain with PTAH. The faint coarse granules scattered in the epithelial cells are also metachromatic, as are the contents of the mucous goblets. 470 ×.

FIGURE 8. Section across a radial pouch, low in the cardiac stomach, showing tall, flagellated epithelium and relative scarcity of secretory cells in the pouch itself. Note also the relationship of the retractor strands to the connective-tissue layer in this region. Periodic-acid-Schiff, Weigert hematoxylin, fast green; 235 ×.

FIGURE 9. Detail of epithelium in a radial pouch. Note the tall, crowded, flagellated cells with their conspicuous brush border, and the well-developed nerve plexus layer through which bases of the epithelial cells extend to attach on the connective-tissue layer. Alcian Blue-carmalum; 470 ×.
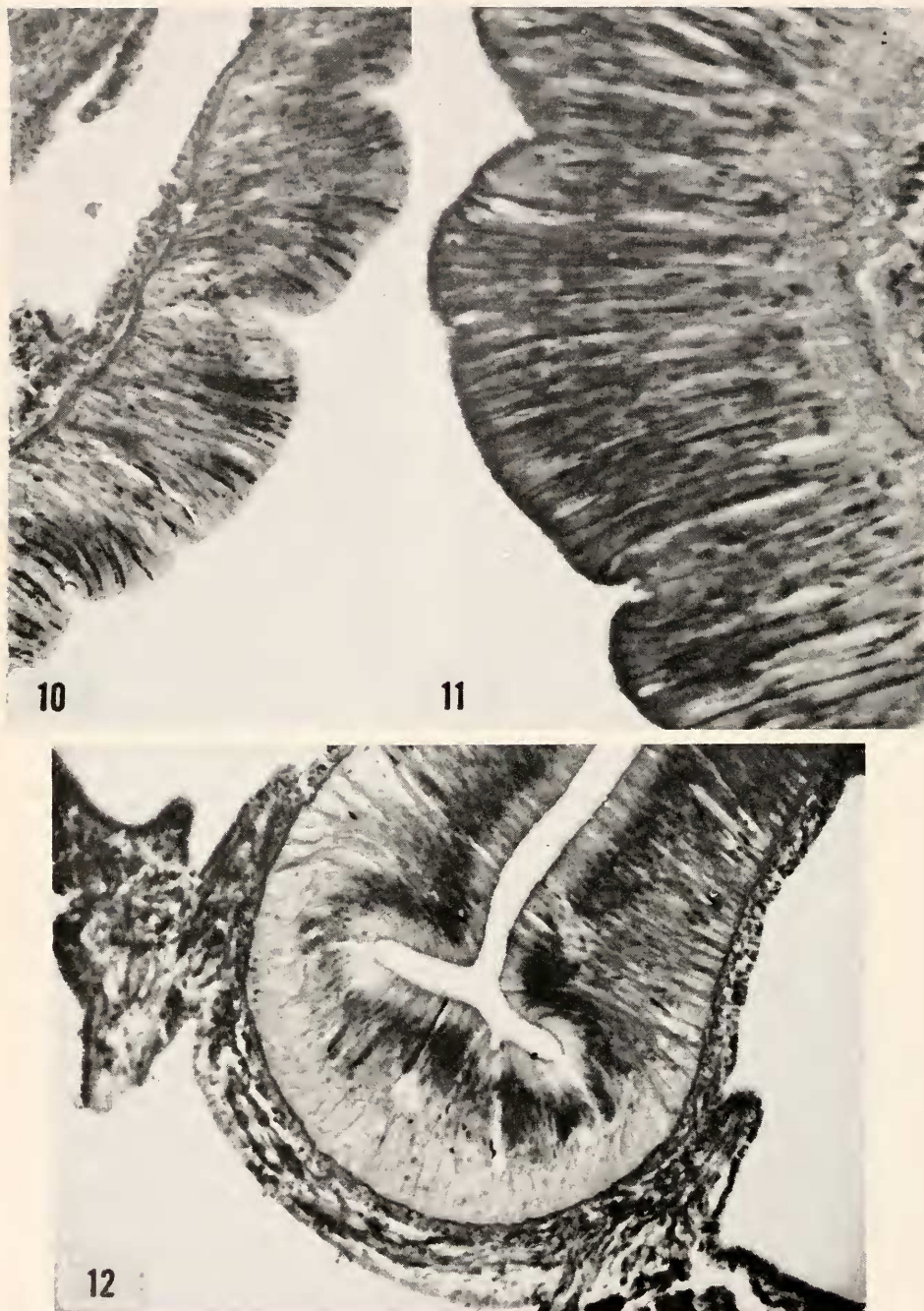
Figure 10. An interradial pouch area, showing abundance of zymogen cells; note also the scanty nature of brush border development and flagella. PTAH; 235 ×.

cells and enter the roots that attach to the surface of the underlying connective-tissue layer. The apical ends of typical cells are provided with a brush border, sometimes rather scanty, about the base of the flagellum. Variations in such typical cells, and in the distribution of different types of secretory cells among them, form the basis of the marked regional specializations characteristic of the digestive tract in *Henricia*.

At the extreme oral end of the cardiac stomach, in the region termed "esophagus" by Hayashi and others, the epithelium lies in numerous folds, supported by lamellar inward extensions from the basal connective-tissue layer. Scattered among the typical epithelial cells here are occasional clumps or strings of secretory granules, and somewhat more numerous tall, flask-shaped mucous goblets with distorted, deeply staining basal nuclei. These features are brought out by staining with phosphotungstic acid hematoxylin (PTAH) and are illustrated in Figure 6. By far the most conspicuous aspect of the epithelium in this region, however, concerns the clear and empty appearance of the apical ends in all of the otherwise typical cells here; PTAH stains nothing (other than flagellary basal bodies) in the distal quarter or so of these cells. In contrast (Fig. 7), treatment of adjacent sections with dilute toluidine blue elicits a most vivid gamma metachromasia in precisely those parts of the cells that fail to stain with PTAH. The same regions are stained by Harris' hematoxylin, selectively colored by Alcian Blue, and even after salivary digestion give a positive reaction with the periodic-acid-Schiff technic. Such staining behavior indicates that the apical portions of the typical cells in this portion of the stomach are filled with masses of an acid mucopolysaccharide, and this is the only place in the entire digestive tract where such materials are found to be so intimately and so copiously associated with "typical" epithelial cells. Metachromatic staining, along with the other reactions described for these cells, is also exhibited by the globular or flocculent contents of the mucous goblets, by material associated with the brush border, and by numerous rather coarse granules or deposits randomly scattered in the deeper parts of the epithelial cells (Fig. 7).

Above this region the metachromatic staining of the typical cells gradually disappears, except for that associated with the brush border, and the wall of the stomach differentiates into its radial and interradial pouches. A clear distinction can usually be made between these two series of pouches on the basis of their epithelial characteristics. In the relatively narrow and deep radial pouches, the epithelium consists almost entirely of typical cells, very crowded, with conspicuous, long flagella and well-developed apical brush borders (Figs. 8, 9); in these areas there are few secretory cells, but some zymogen cells are present and some mucous cells containing flocculent secretion. By contrast, the larger and broader interradial pouch areas exhibit an epithelium very rich in mucous goblets and with relatively large numbers of zymogen cells (Figs. 10, 11). Although the typical

FIGURE 11. Mucous gland cells in an interradial pouch area comparable with that shown in Figure 10. Periodic-acid-Schiff after salivary digestion, Weigert hematoxylin, fast green. Note the tall, slender, deeply-staining mucous goblets, and the diffuse positive stain in the distal parts of the epithelium after removal of all glycogen. 470 ×.

FIGURE 12. Radial gutter in cardiac stomach, upward extension of a radial pouch. Tall, crowded, conspicuously-flagellated cells, well-developed nerve plexus layer; note also the large, darkly-stained mucous goblet. PTAH; 235 ×.
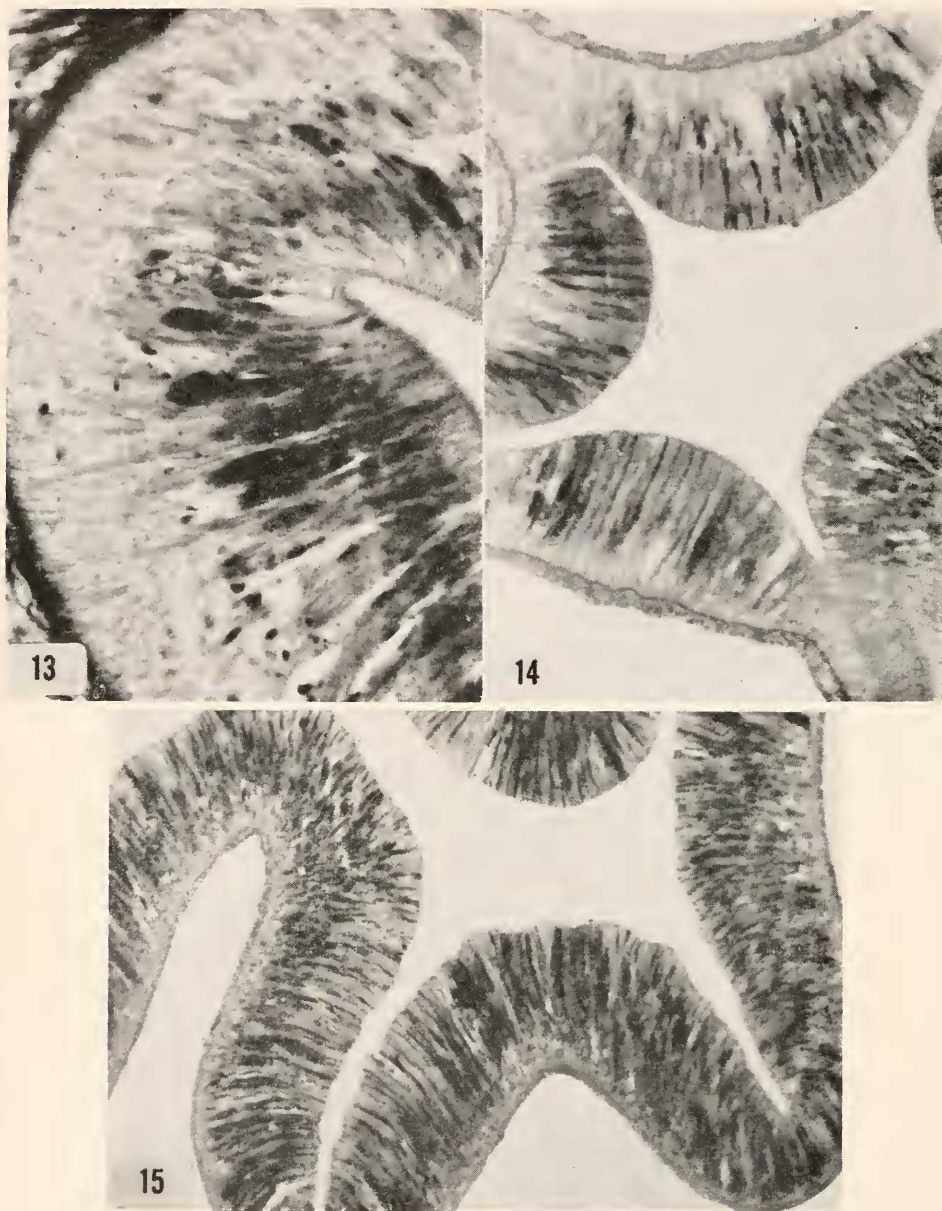
FIGURE 13. Detail of a region similar to that shown in Figure 12. Note bulbous mucous goblets, with scattered spindle-shaped bodies deep in the epithelium (*cf.* Fig. 16). PTAH; 470 ×.

FIGURE 14. Frontal section through the central aperture leading into the pyloric stomach, showing secretory type of epithelium with numerous mucous glands, scanty brush borders and flagella. PAS-Weigert-fast green, salivary digestion; 235 ×.

FIGURE 15. Frontal section through portion of radial reservoir of the pyloric stomach, stained to reveal the abundance of zymogen cells in this region. PTAH; 235 ×.

cells that are found here show flagella on close examination, these are sparse and relatively short, and the brush borders are scanty. These general distinctions in epithelial characteristics follow consistently upward through the cardiac stomach; the crowded, flagellated, conspicuously brush-bordered cells of the radial pouches continue upward through the radial gutters, crossing into the pyloric stomach as tracts leading to the marginal openings in its walls, with the addition of a large, dense, bulbous type of mucous gland cell (Figs. 12, 13). The richly secretory epithelium of the interradial pouch areas, with its short, scanty flagella and brush borders, extends to clothe the centrally-directed vesicles of the cardiac stomach and even to furnish the characteristic lining of the floor and walls of the branching pyloric stomach (Fig. 14). Zymogen cells are numerous throughout, but particularly in the radial reservoirs (Fig. 15). All of these areas also contain very abundant mucous cells, varying from tall, slender goblets with fine granular secretion to large, flask-shaped glands filled with coarse, homogeneous globules, resembling those encountered in the radial gutters. These may represent different secretory phases of a single basic type of mucous gland. In the central folds between radial branches of the pyloric stomach the epithelium exhibits an interesting feature; interspersed among the upper ends of the tall, crowded epithelial cells lie small, spindle-shaped bodies staining deeply with the hematoxylins or with carnalum. They increase in abundance in the folds of the radial reservoirs and are particularly numerous and conspicuous in areas where opposite side walls are closely apposed (Figs. 16, 17a, 17b). They are, at least in these areas, almost entirely limited to the upper third or quarter of the epithelium and so are in reasonable proximity to the lumen. These elements resemble most strongly the bodies described by Smith (1937) as primary sense-cells in *Marthasterias;* they are very much like the sense cells Smith found in the radial nerve cord and bear a less striking resemblance to the cigar-shaped nuclei of the cells he interprets as representing the same elements in the lining of the stomach (see also Anderson, 1954). The deeply-staining spindles in my preparations of *Henricia* are evidently nuclei, sometimes granular but most frequently dense and homogeneous. The cytoplasm to which they belong cannot be distinguished, crowded as these bodies are in the great profusion of secretory cells (Figs. 17a, 17b); it probably consists, as Smith's Figure 5 suggests (1937, p. 123), of slender, fibrous processes running downward from the free border of the epithelium into the nerve plexus layer below. Diligent search for similar bodies in the cardiac stomach reveals a number of spindle-shaped nuclei deep in the epithelium of the flagellated tracts, usually in association with large mucous glands (Fig. 13).

In each radial reservoir, an abrupt line of transition is evident where the richly secretory side-wall epithelium gives way to the conspicuously-flagellated typical-cell epithelium (Fig. 18) that covers the roof of the pyloric stomach and continues as the lining of the intestine.

The "granulated gland cells well-stained by eosin" mentioned by Hayashi (1935, p. 10) as a component of the epithelium in the cardiac stomach, and as being present in suddenly increasing numbers in the pyloric stomach, cannot be identified, unless they correspond to what I have called zymogen cells. In my preparations the zymogen granules stain neither with eosin nor with Harris' hematoxylin; they appear as clear, refractile spherules crowded in an eosinophilic ground cytoplasm. This, it will be noted, may offer an answer to the puzzling
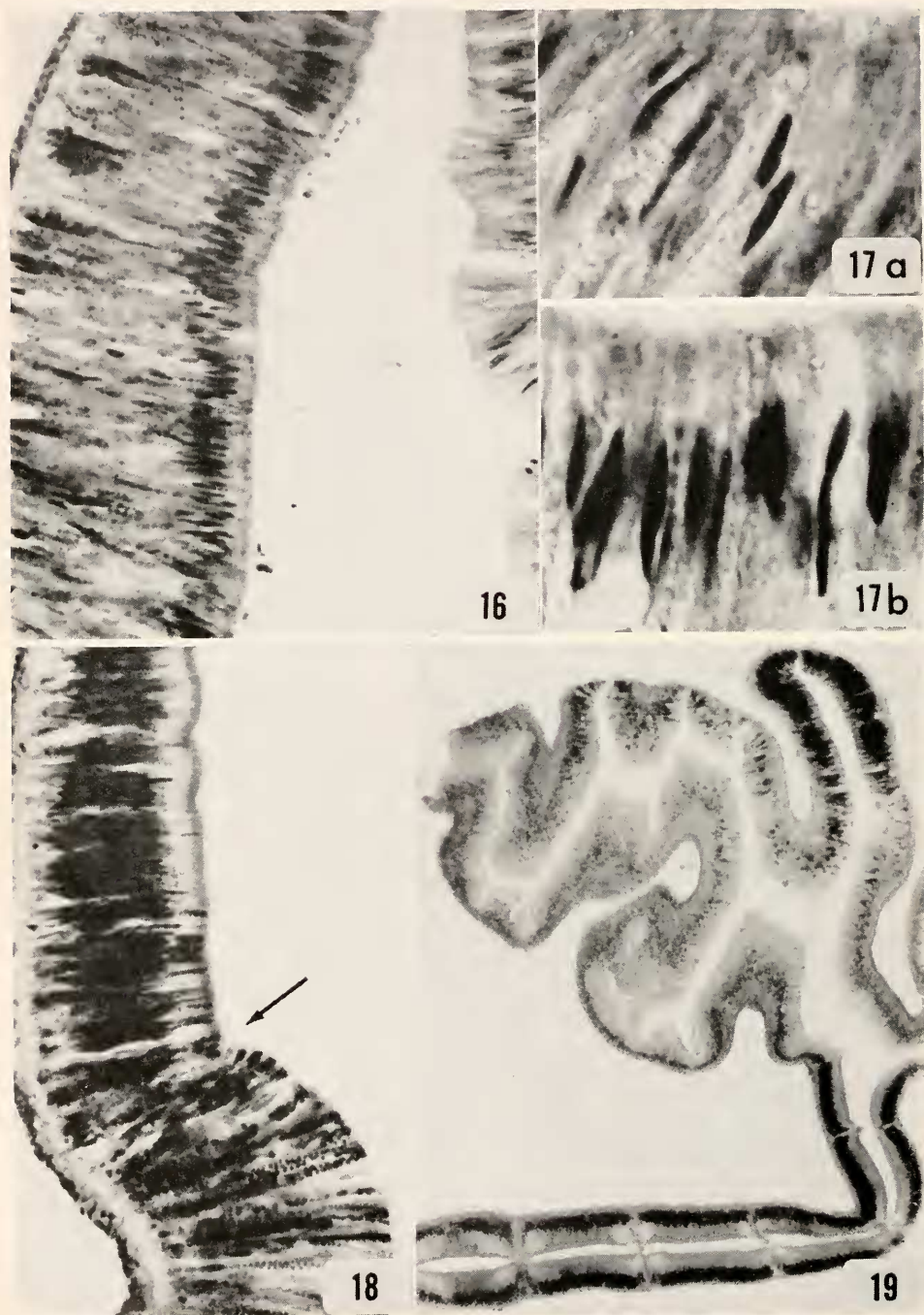
FIGURE 16.   Side wall of a radial reservoir, showing abundance and localization of spindle-shaped nuclei interpreted as pertaining to sensory cells.   PTAH; 470 ×.

problem: the *cells*, as Hayashi says, are granulated and do stain well with eosin; but the granules themselves are not eosinophilic.

The duality so evident in the gross anatomy of the pyloric caecum-Tiedemann pouch complex is revealed also in the histology of the organs. The caecum and its median duct share epithelial characteristics with the central pyloric stomach and its radial reservoirs, while the histological affinities of the pouch are, not surprisingly, with the lower part of the pyloric stomach and even with the radial pouches and gutters of the cardiac stomach. It will be recalled that these areas form continuous flagellated tracts in the stomach, leading directly into the openings forming the roots of the paired Tiedemann pouches. Figure 19 illustrates the striking histological contrast between the upper and lower parts of the caecum-pouch complex.

As each radial reservoir of the pyloric stomach tapers to form the median duct of its caecum, the proportion of zymogen cells in its epithelium increases to a maximum. The roof and side-walls of this median duct present a greater concentration of zymogen cells than any other part of the caecum; the folded walls of the lateral diverticula branching from the duct always contain large numbers of such cells (Figs. 19, 20), but nowhere in these lateral areas do they occur in such profusion as in the median duct. In the scattered zymogen cells of the diverticula, but not in the crowded ones of the duct, the masses or strings of granules are commonly accompanied by clear vacuoles (Fig. 21), a condition previously noted in the caecal zymogen cells of *Asterias forbesi* (Anderson, 1953) and still without explanation. The epithelium of the median duct, and to a lesser extent that of the lateral diverticula, also contains numerous mucous goblets like those found in the pyloric stomach, as well as a considerable representation of the dense spindle-shaped bodies interpreted as pertaining to sense-cells. These last are very difficult to find in the lateral diverticula and particularly so in the outer parts.

Beyond these special features, the pyloric caeca present little to distinguish them histologically from those of *Asterias forbesi* (Anderson, 1953). Most of the cells making up the epithelium of the lateral diverticula are relatively undifferentiated, with flagella and apical brush borders, and evidently function chiefly as absorptive and storage cells. Most of them contain several to many coarse, granular bodies, usually lying below the level of the nucleus (Fig. 21). These are highly basophilic and are Schiff-positive after periodic acid oxidation, resisting salivary digestion; they are not metachromatic and do not stain with Alcian Blue. Although this is insufficient for specific characterization, the staining behavior of these bodies suggests that they consist of some type of mucopolysaccharide that may be serving as a nutritional reserve. In contrast to the storage cells in the caeca of *Asterias*, those of *Henricia* appear to contain very little glycogen

FIGURES 17a, 17b. Details of sense-cell nuclei. PTAH; 1100 ×.

FIGURE 18. Sharp transition zone (arrow) between richly secretory side-wall epithelium of radial reservoir (*below*) and current-producing, flagellary epithelium of roof (*above*). PTAH; 470 ×.

FIGURE 19. Overall cross-section of a caecum-pouch complex; the pouch (*below*) normally hangs straight down (*cf.* Fig. 5) but has been bent over in histological processing. Note the marked localization of deeply-staining zymogen cells in the median caecal duct (*upper right*), and the arrangement of the parallel flagellated channels traversing the pouch from the gutter (*lower left*) to the lower part of the median duct. Seam-cell adhesions separate adjacent channels. PTAH; approximately 75 ×.
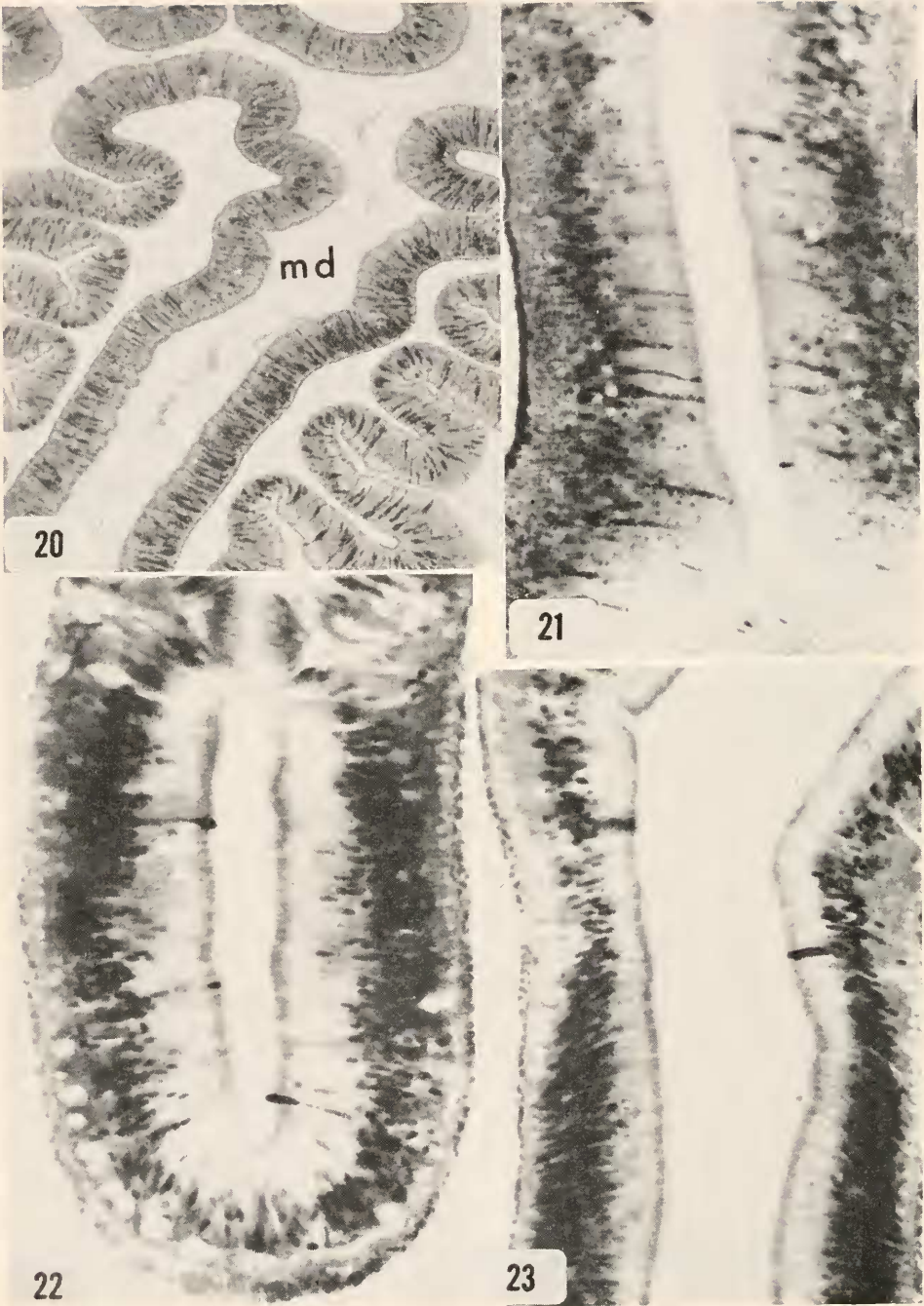
FIGURE 20. Frontal section through side wall of median duct, showing relationship between its lumen (*md*) and the lateral diverticula branching from it. Note also distribution of zymogen cells (*cf*. Fig. 19). PTAH; approximately 75 ×.

or lipid. This condition is perhaps related to the fact that my specimens of *Henricia leviuscula*, from which tissues were taken for the periodic-acid-Schiff and Sudan black technics, were collected just as they entered their breeding season. Although detailed studies involving *Henricia* have not been made, the work of Greenfield, Giese, Farmanfarmaian and Boolootian (1958) has conclusively demonstrated for two other starfishes that glycogen and particularly lipids are transferred from storage in the caeca for utilization in the ripening gonads as the breeding season approaches.

Along a line at the lower edge of the median duct, below the origins of the lateral diverticula, the epithelium changes abruptly (Figs. 19, 23). This line marks the junction between Tiedemann's pouch and the caecum proper. Within the pouch, the epithelium of the side walls is almost a pure population of "typical cells"; zymogen cells are few and widely scattered, and mucous cells, as will be seen, are strictly localized according to a definite pattern. The typical cells are extremely crowded and laterally compressed; the nuclei lie in a wide band of varying levels, a brush border is well developed, and each cell bears one or two (difficult to determine) long and powerful flagella, with conspicuous, elongate basal bodies and intracellular fibrils.

The floor of Tiedemann's pouch is narrow, formed by a gutter leading outward from one of the marginal openings low in the pyloric stomach. The epithelium lining this gutter contains an abundance of large mucous gland cells of the dense, bulbous type, their swollen cavities packed with globular secretion masses distorting their own nuclei and crowding the neighboring epithelial cells in all directions (Figs. 22, 24). Deep in the epithelium, between the mucous goblets, lie a considerable number of spindles, like those seen in similar locations in the cardiac stomach.

At regular intervals, bands of the crowded mucous-epithelial cells pass diagonally upward from the gutter to the lower margin of the caecum above, traversing the normal epithelium of the side walls of the pouch as a series of parallel striations clearly visible through the wall of the organ (see Figure 5). A transverse section of the caecum-pouch complex, such as that shown in Figure 19, cuts across several of these striations; examination reveals that each is a line of adhesion between corresponding bands of mucous-epithelial cells on facing walls of the pouch. These seams divide the pouch into approximately 30 parallel channels (in an average-sized animal), running diagonally upward from the gutter to join the median duct of the caecum, each channel lined on both its side walls by a type of epithelium evidently highly specialized for the production of powerful flagellary currents. The seams or lines of adhesion separating adjacent channels involve bands of tissue several to many cells wide, in which the nuclei in both of

FIGURE 21. Detail of epithelium in a lateral diverticulum. Note vacuoles associated with zymogen granules, and the abundant coarse granules below the nuclear level, interpreted as mucopolysaccharide deposits. PTAH; 470 ×.

FIGURE 22. Cross-section of the oral gutter of Tiedemann's pouch, bounded at top by an adhesion-seam. Note the crowded current-producing cells in the side wall, the few and scattered zymogen cells, the abundant mucous gland cells in the floor of the gutter (*cf.* Fig. 24), and the thickened tracts (clear basal circles) of the nerve plexus layer in the floor of the gutter. PTAH; 470 ×.

FIGURE 23. Transition zone marking the junction between Tiedemann's pouch and the pyloric caecum, where the current-producing typical-cell epithelium of the pouch gives way to the secretory and storage-cell epithelium of the caecum. PTAH; 470 ×.
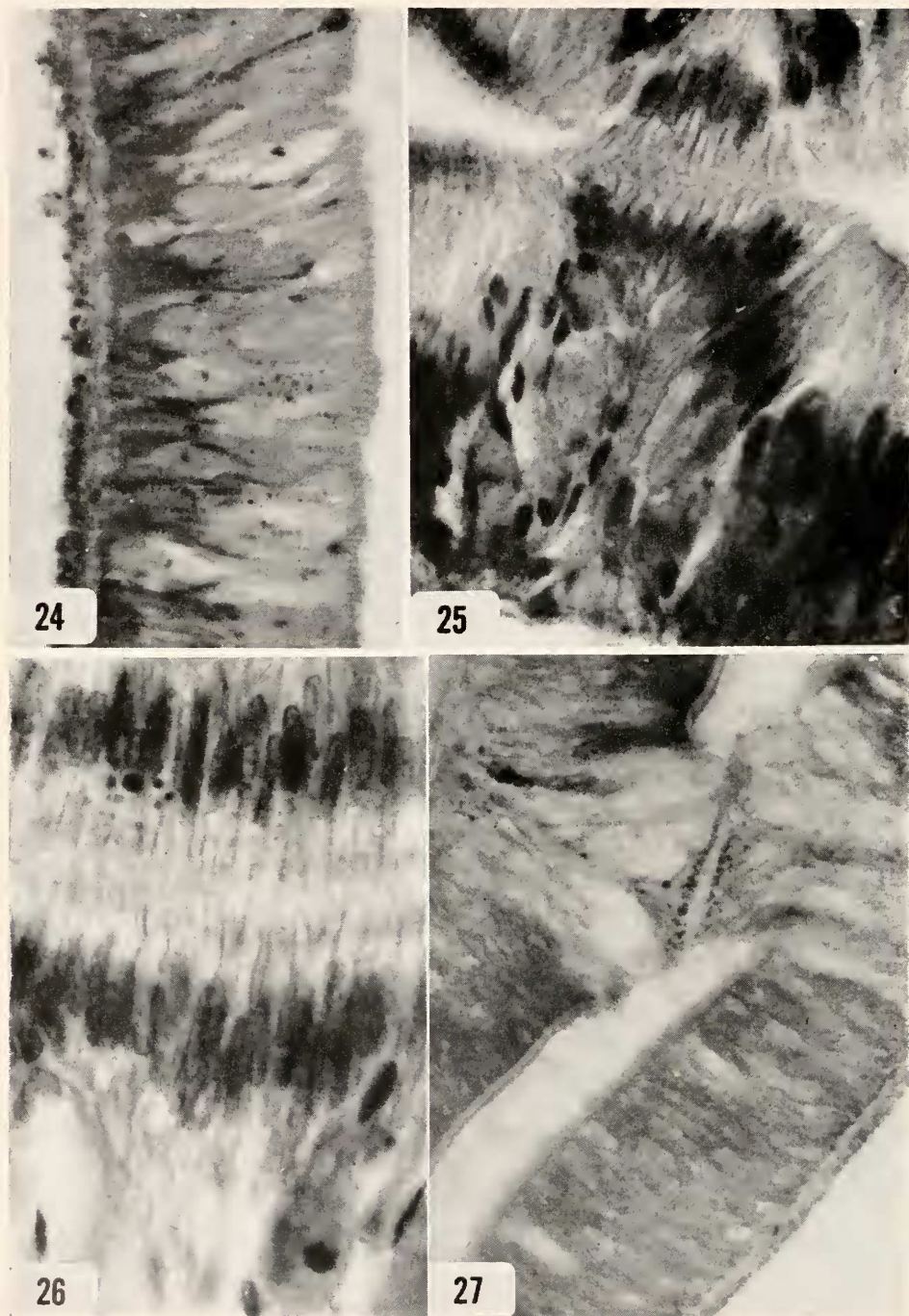
Figure 24. Frontal section, side wall of oral gutter in Tiedemann's pouch, to show the abundance of huge, bulbous mucous glands characteristic of this area. Note also spindle-shaped nuclei scattered deep in the epithelium. PTAH; 470×.

the apposed epithelia lie exceptionally high in the tissue. In section (Fig. 25) they give the impression of having been heaved or herniated outward from the basement membrane by pressure from the swelling bands of mucous gland cells between which they are confined.

The localization of the herniated seam-cells and their flanking bands of mucous cells, and the regular alternation of these zones of adhesion and the flagellated channels which they separate, are clearly shown in Figure 19. Although their nuclei have been raised almost to the level of the free edge of the epithelium, the seam-cells retain their attachment to the basal connective-tissue layer by way of elongated, compressed cytoplasmic stalks in which supporting fibrils are strongly developed. These intracellular fibrils continue upward past the nuclear level and form a characteristic and conspicuous feature of the distal ends of the joined cells (Figs. 25, 26). They do not, however, cross the plane of fusion to join the fibrils of cells in the opposite walls, and I have seen no other evidence of actual cytoplasmic continuity between the adherent cells; in favorable preparations a distinct double membrane can be observed at the seam-line. Nevertheless, the adhesion-seams are firm, close, and evidently permanent; when the tissue is broken or torn at a seam in the course of histological manipulations, it is noteworthy that the seam almost never tears at the line of fusion but rather just below the nuclei of the seam-cells of one side or the other.

The distal ends of the seam-cells contain a number of moderately coarse granular deposits which in their staining behavior resemble the Schiff-positive globules of the storage cells in the pyloric caecum. As in the caecum, very little glycogen or lipid appears in any of the cells of Tiedemann's pouch. Oddly, the only conspicuous sudanophile inclusions in the pouch areas lie in the distal ends of the seam-cells, appearing as discrete droplets scattered in the supranuclear cytoplasm (Fig. 27). The significance of lipid localization in these highly specialized and aberrant cells is problematic.

The sense-cell spindles identified deep in the epithelium of the gutter accompany the adhesion-bands also. Here they lie among the swollen mucous goblets (Fig. 25) and are often compressed against the elongate, fibrous stalks of the seam-cells. Smith has noted that in *Marthasterias* the sense-cells occur principally in those areas of the gut where the subepithelial nerve plexus layer is particularly well developed. In this connection it is of interest that in *Henricia* the floor of the gutter is underlain by several notably thickened tracts of the plexus layer (Fig. 22), and that similar thickenings accompany the specialized adhesion-tracts and unite with conspicuously well-developed areas of the plexus layer along the line of attachment between Tiedemann's pouch and the caecum (Fig. 23). The correspondence in distribution between the thickenings of the plexus layer and the

FIGURE 25. Detail of a seam-cell adhesion-band in Tiedemann's pouch. Note the apparent herniation of the seam-cell nuclei upward, and the attachment of these cells to those opposite in the epithelium across the lumen. The seam-cells maintain attachment to the basal connective-tissue layer; note the band of bulbous mucous goblets flanking the seam-cell zone on both sides, scattered sense-cell nuclei, and crowded typical-cell epithelium in channels to left and right. PTAH; 1100 ×.

FIGURE 26. Distal ends of apposed seam-cells. Note that the intracellular fibrils are not continuous across the line of fusion. PTAH; 2100 ×.

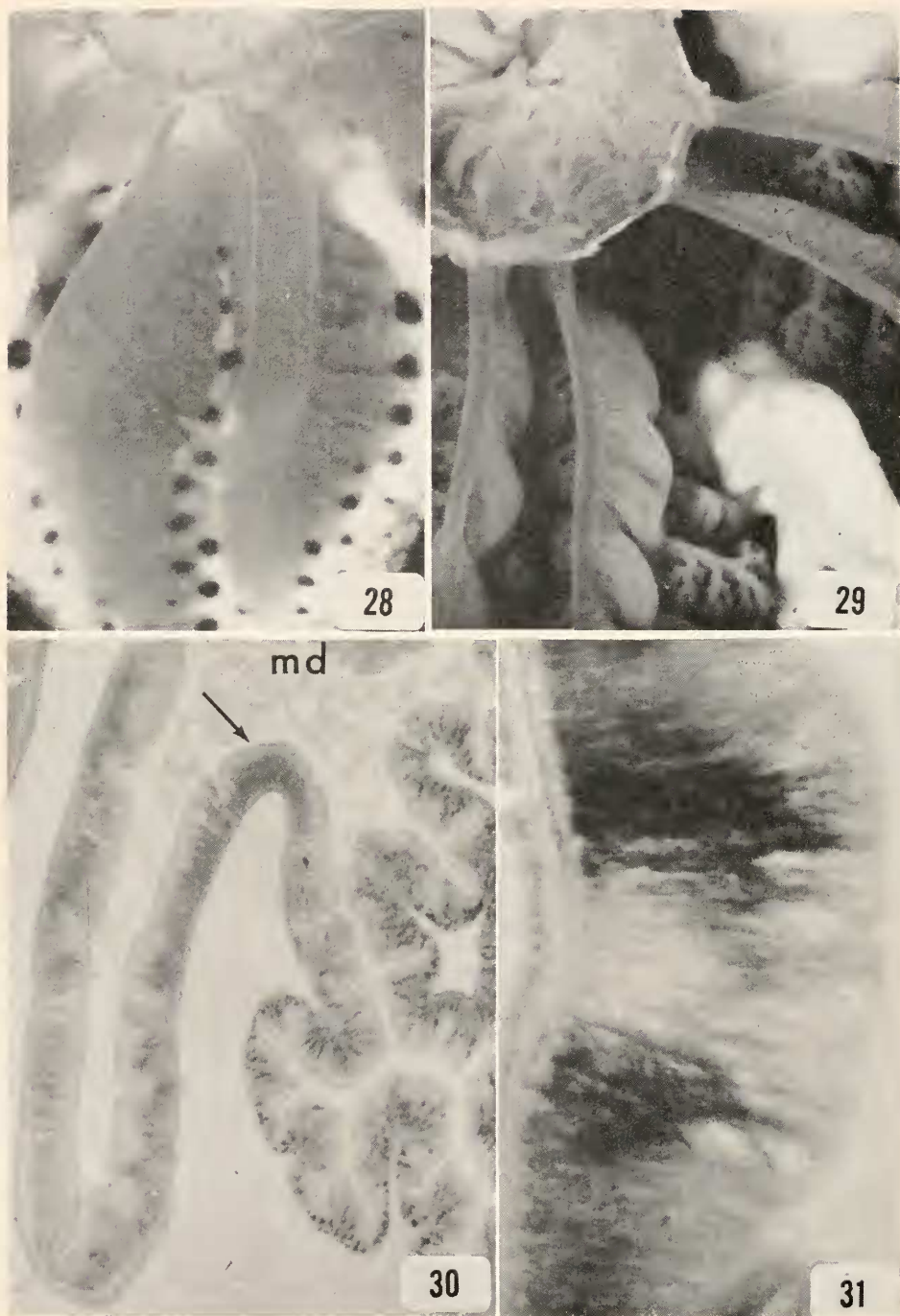FIGURE 27. Sudanophilic droplets in distal ends of seam-cells. Sudan black-carmalum; 470 ×.

FIGURE 28. A pair of caecum-pouch units in *Patiria*, from below. Note the separate origins from the pyloric stomach, and the broad, bag-like nature of the Tiedemann's pouches. Dissection of a living specimen, approximately 5 ×.

concentrations of sense-cell spindles in Tiedemann's pouch seems unlikely to be merely coincidental.

C. Function

The relatively small size of the cardiac stomach, and the absence of voluminous gastric pouches, make it appear improbable that feeding in *Henricia* involves eversion of the stomach to the extent characteristic of *Asterias* or *Patiria*. Living specimens at rest are frequently observed with the mouth widely open, with folds of the lower cardiac stomach lying over the peristomial lips. Within the stomach the lumen is largely occupied by the swelling vesicles of the upper cardiac stomach, framing the narrow, stellate opening into the pyloric stomach. In some specimens, these vesicles appear partially everted through the mouth, where they form lobe-like structures extending only about a millimeter. It is to be noted that the stomach is provided with a stout muscular and fibrous retractor harness which, while differing markedly from that described for *Asterias* and *Patiria* (Anderson, 1954, 1959), still appears much too well-developed to be merely an anchor for the resting stomach. The action of the stomach suggests that the retractors function in securing the vesicular lobes, adjusting their degree of eversion, and maintaining the folds or gutters between them.

The organization of the various flagellated tracts, ducts, and channels suggests that the digestive tract in *Henricia* is particularly well adapted for the production of currents and the transport of suspended particles. The existence of such currents, and their intricate interrelationships within the digestive tract, can be demonstrated by the use of suspensions of India ink or stained yeast cells. Particles move rapidly upward through the radial pouches and gutters of the cardiac stomach, into the pyloric stomach, and out through the marginal openings into Tiedemann's ducts. In dissected specimens, suspensions introduced into one of these ducts are observed to pass distally with astonishing rapidity through the gutter of the pouch, from which successive streams are diverted and directed upward through all the diagonal flagellated channels into the median duct of the pyloric caecum above. Reaching this, particles move into the lateral diverticula of the caecum, up their side walls, and back across their roofs into the aboral part of the median duct. Here, a strong centrally-directed current streams inward, moving the suspension across the folded surfaces of the radial reservoir and into the narrow central lumen of the pyloric stomach. Currents converging here from all the radial reservoirs pass downward into the lower part of the pyloric stomach, where particles again come under the influence of the radial flagellated gutters and the currents setting towards the marginal openings and into Tiedemann's

FIGURE 29. Detail of similar structures. Note the oral gutter on the margin of Tiedemann's pouch, and the fold-patterns traversing the side walls. Approximately 10 ×.

FIGURE 30. Cross-section of a caecum-pouch complex. Note the absence of flagellated channels or adhesion seams, the relationship between the broad lumen of the pouch and the median duct (*md*) of the caecum above, and the crowded band of typical cells (*arrow*) at the junction between pouch and caecum. Zymogen cells are also visible in the epithelium of the lateral diverticula. PTAH ; 75 ×.

FIGURE 31. Sudanophilia in side-wall epithelium of Tiedemann's pouch, *Patiria*. Note that the mucous-gland patch (clear center area) is flanked on each side by a band of highly sudanophilic cells which gradually fades into a typical-cell epithelium. These alternating bands are responsible for the appearance of parallel folds in the side walls. Sudan black-carmalum ; 470 ×.

ducts. A complete and very active circulation through the digestive tract is thus maintained, featuring one-way transport of solutions or suspensions by specifically-directed flagellary currents. Sorting mechanisms undoubtedly occur; in the radial reservoirs, for example, selected particles are probably carried across the roof of the pyloric stomach and into the intestine for elimination. But it is clear that a given particle, until thus eliminated or until completely digested, can make innumerable circuits through the secretory regions of the digestive system. There are regional differences in transport velocity—currents in the lateral diverticula of the caeca, for instance, move much more slowly than those in Tiedemann's ducts and pouches—but there appear to be no static areas and no chambers in which large masses of ingested food can lie while undergoing dissolution.

D. *Tiedemann's pouches in other starfishes*

As pointed out by Cuénot (1887), members of the Family Echinasteridae (*Echinaster, Henricia*) share with those of the Family Asterinidae (*Asterina, Patiria*) conspicuous development of the organs we are calling Tiedemann's pouches. In *Patiria miniata,* for example, the paired caeca of a single ray originate separately from the pyloric stomach, and a well-developed, elongate pouch hangs from the oral midline of each caecum (Figs. 28, 29). The lower margin of the pouch is formed by a tubular gutter, taking its origin, like the similar structure in *Henricia,* from an opening in the wall of the stomach just above the circumferential fibrous girdle. As in *Henricia* also, the walls of the pouch are traversed by a regular series of parallel folds, visible externally, that run diagonally upward from the gutter to the median duct of the pyloric caecum above. The lateral diverticula of the caecum form complexly folded pockets arising at intervals from the lateral-aboral walls of the median duct. Although superficially similar, the caecum-pouch complexes in *Patiria* and *Henricia* present many fundamental differences. *Patiria* lacks, for example, the specialized portions of the pyloric stomach termed radial reservoirs in *Henricia;* Tiedemann's pouch and the median duct of the caecum open into the pyloric stomach by a common aperture, tall and narrow but not divided. Histological comparison reveals further contrasts (Fig. 30). Within the caecum, zymogen cells, mucous gland cells, and storage cells are more or less uniformly distributed, without the marked segregation of zymogen cells in the median duct so conspicuous in *Henricia.* It will be noted also that Tiedemann's pouch is more broadly attached below the caecum, and that the pouch itself is broader and more bag-like. This is explained by the fact that, as Figure 30 shows, the opposite walls of the pouch are not held together by mucous-epithelial adhesions as in *Henricia* but are only approximately parallel and not closely apposed. The conspicuous striations in the walls, superficially so similar to those of *Henricia,* are produced by parallel bands of large, crowded mucous gland cells alternating with bands of extremely crowded, very tall "typical" cells. A notable concentration of these non-secretory cells is always found in the zone of attachment where Tiedemann's pouch joins the median duct of the caecum. No zymogen cells are found in the pouch. The distribution of lipids is significantly different from that in the pouch of *Henricia.* All of the crowded typical cells show accumulations of sudanophile droplets in their basal portions, even extending through the thin strands that penetrate the thick nerve plexus layer and

insert on the connective-tissue sheet. (Fig. 31). The mucous gland cells contain no notable lipid deposits, but each of the mucous bands is flanked by strips in which the typical cells contain exceptionally high concentrations of lipid droplets. These fade gradually into the normal typical cells in the areas between the mucous bands. There are no cells here comparable to the herniated seam-cells of *Henricia* with their apical concentrations of sudanophile droplets.

Suspensions of stained yeast cells introduced at the opening leading into one of the pouches are carried through a pattern of circulation very similar to that observed in *Henricia*. Even though the walls of the pouch do not adhere to form separate channels, the concentrated flagellary bands are capable of producing rapid currents that distribute materials along the entire length of the median duct. There are no quiet or stagnant areas; whatever enters the pouch moves immediately into the caecum, then back to the pyloric stomach and outward through the pouch again. The general pattern described by Irving (1924) in the caecum-pouch complex is verified, although the anatomical relationships shown in his figure (p. 117) are inaccurate.

Without going into detail, brief anatomical and histological examination of the digestive tract of *Asterina gibbosa* shows that the features of its pyloric caecum-Tiedemann pouch complex are very similar to those of its close relative *Patiria* and differ in the same ways from those of *Henricia*.

A figure sketched by Richters (1912) in his study of regeneration in *Linckia* led me to suspect that the pyloric caeca of this starfish might also bear Tiedemann's pouches, although this has not been reported in the literature and *Linckia* is placed in a different order (Phanerozonia) from that to which the asterinids and echin-asterids belong (Spinulosa) (see Hyman, 1955, pp. 334, 336–337). Preliminary studies on preserved specimens of *Linckia guildingi* reveal that Tiedemann's pouches are indeed present and are larger and better-developed than those of any other species examined so far. They extend almost to the distal ends of the long pyloric caeca, and their proximal ducts are separated by partitions from specialized portions of the pyloric stomach resembling the radial reservoirs of *Henricia*. Transverse sections of the pouches show that adhesion-bands similar to those of *Henricia* divide the pouch into separate flagellated channels. The gutter forming the oral margin of the pouch is divided by a fold arising from its floor, which externally encloses a stout band of muscle fibers. Altogether, although details have not been exhaustively studied, it is evident that the caecum-pouch complex in *Linckia* is strikingly similar in its fundamental characteristics to that described in *Henricia*. This is the more interesting in view of the wide taxonomic gap that apparently separates the two genera.

Astropecten, in which Tiedemann (1816) originally described the pouches that now bear his name, has very small ones extending a centimeter or less along the oral side of the median duct of the caecum. Their side walls show a few moder-ately developed parallel striations, but in the preserved material on which I have made a preliminary study these do not form firm adhesions across the lumen.

Discussion

There are many anatomical and histological differences between the organs of the digestive tract in *Henricia* and those of other starfishes in which details

have been described. The small size of the cardiac portion of the stomach, the large size and peculiarly branched structure of the pyloric portion, the conspicuous development of the rectal caeca, and other features, were noted by Hayashi (1935). Further, the cardiac stomach of *Henricia* lacks any hint of the elaborately branching patterns of flagellated gutters, with accompanying ramifications of the retractor strands and corresponding localizations of specialized epithelial cells, characteristic of the cardiac stomach in *Asterias, Pisaster, Pycnopodia,* and *Patiria* (Anderson, 1954, 1959). Lacking these, the stomach of *Henricia* is not, however, without specializations of its own, such as the so-called esophageal pouches and the alternating gutters and vesicles at higher levels, with their marked histological distinctions. Other histological peculiarities are common in various parts of the digestive tract. For instance, areas in the cardiac stomach and almost the whole of the pyloric stomach are lined with zymogen cells; in contrast, the zymogen cells of *Asterias forbesi* and *Patiria miniata* are found only in the pyloric caeca. Within the caeca of *Henricia,* the startling concentrations of zymogen cells in the walls of the median ducts are unique; in *Asterias,* this area is given over to a population of tall, crowded, current-producing cells interspersed with mucous goblets, and the zymogen cells are restricted to the lateral diverticula.

Such instances of structural contrast could be multiplied, all leading to the conclusion that in starfishes, as in other animals, corresponding parts of the digestive system, clearly homologous, may be adapted to diverse functions in relation to differences in food and in feeding methods. The food habits and feeding mechanisms of *Asterias* and similar forms are reasonably well understood; that they are probably not at all like those of *Henricia,* which are unknown, is indicated by the conspicuous structural differences revealed by detailed study.

In general, the specializations noted in *Henricia* seem to involve a tendency to segregate tissues with predominantly secretory functions in areas more or less distinct from those serving primarily for current production. Further, while the transport of materials through the gut by flagellary currents is common to all starfishes, in *Henricia* this function has been raised to a peak of efficiency by the development of the special modifications of the pyloric stomach called Tiedemann's pouches. By means of these elaborate organs, suspensions or solutions brought to them by the flagellary tracts of the stomach are very rapidly distributed to the secretory and absorptive areas of the pyloric caeca and pyloric stomach, and maintained in repeated circulation through these areas until digested, absorbed, or eliminated.

Studies elucidating the current-patterns maintained within the digestive tract have been made on a variety of asteroids, including *Asterias rubens, Solaster papposus, Porania pulvillus,* and *Astropecten irregularis* (by Gemmill, 1915); *Patiria miniata* (by Irving, 1924); and *Asterias forbesi* (by Budington, 1942). It is noteworthy that in all of these species, of diverse taxonomic affinities, the patterns are reasonably similar in general outline, with minor variations related to anatomical differences. In all, currents flow in the oral-aboral direction from cardiac to pyloric stomach; radially across the floor of the pyloric stomach and outward along the oral sides of the pyloric ducts, continuing on the oral side of the median duct in each caecum; in a circular fashion through the lateral diverticula and back to the median duct, this time aborally; and finally returning toward the

pyloric stomach again in the aboral part of this duct.   In the Asteriidae, particularly, the pyloric duct is a restricted passage; within it, however, currents must be maintained both centrifugally and centripetally, the one current running on its oral side, the other on its aboral side.

It is obvious that the feeding and digestive activities of the predatory, carnivorous starfishes in this family place no demands upon their transport mechanisms that are not satisfied by the system as it exists.   Yet, if one speculates upon ways in which this system might have developed to operate more efficiently for the maintenance of directed currents in the standard pattern, one is likely to be struck first by the existence of the bottle-neck at the pyloric duct.   For increased efficiency, the pyloric duct should be larger, it would seem, or at least taller, so that the centrifugal and centripetal streams might be more widely separated. Alternatively, a continuous partition should be provided, set horizontally between the floor and the roof of the duct, for complete isolation of the two currents. In effect, it will be noted, the pyloric ducts of *Patiria* embody the former principle, while those of *Henricia* follow the latter.   These considerations seem to justify the conclusion that in both *Patiria* and *Henricia* the functions of the digestive system have placed a higher premium upon efficiency of the flagellary transport mechanisms than is the case in *Asterias* and its close relatives.

Below and distal to the partition that divides the pyloric duct in *Henricia*, Tiedemann's pouch has evolved into a hydrodynamic organ or flagellary pump of prodigious effectiveness.   Its design involves close-set, strongly-flagellated side walls, strengthened, reinforced, and held at what we may assume to be an optimal distance from one another by the unique mucous-epithelial seams, which also break up the otherwise broad epithelial expanse into channels set in regular parallel array.   These features make it possible for the organ to develop what must be a considerable suction, as the force developed in all of the 30 or so flagellated channels is transmitted to the upper cardiac and lower pyloric stomach by way of the restricted Tiedemann's duct.   Fluids and suspensions are drawn rapidly from the stomach through this duct and are ejected at reduced velocity along almost the entire length of the median caecal duct, into which the channels of Tiedemann's pouch lead.   It is reasonable to assume that the development of the 10 Tiedemann's pouches as organs furnishing the principal motive power for circulation through the entire digestive tract brought about the emancipation of areas in the pyloric stomach, pyloric ducts, and median caecal ducts from the primarily flagellary functions they must serve in the Asteriidae, and their development of the richly secretory epithelium that is their chief characteristic in *Henricia*.

In contrast, Tiedemann's pouches in *Patiria* are, as we have seen, broad and bag-like, with no adhesion-seams to hold their side walls in apposition and only their similarities in origin and anatomical relationships to suggest that they are related to the pouches of *Henricia*.   The alternating diagonal bands of mucous glands and typical flagellated cells undoubtedly approach in functional significance the parallel channels of *Henricia*, to which they show a superficial resemblance in external appearance.   Irving (1924) concluded that Tiedemann's pouches in *Patiria* represent regions specialized for distribution, and all observational evidence bears out this supposition.   It is to be doubted, however, that these relatively crudely-developed

organs even approach in efficiency the more elaborate ones of *Henricia*. The enlargement of the pyloric duct and the median duct of the caecum resulting from the development of the pouch in *Patiria* must represent an advance over the condition that exists in *Asterias,* but one is led to the conclusion that as organs of distribution, or flagellary pumping organs maintaining circulation within the digestive tract, the pouches of *Henricia* are far superior to those of *Patiria*.[2]

Many features of anatomy and histology in the digestive system of *Henricia*— the small size and doubtful eversibility of the cardiac stomach, the absence of any sizable chambers in which masses of food might lie while undergoing digestion, and the obviously high degree of specialization of mechanisms for maintaining flagellary circulation, among others—suggest most strongly that this animal is dependent in its nutrition upon suspended particulate matter rather than upon predation or any other form of macrophagy. The following experiment was performed as a preliminary test of this hypothesis. Two specimens of *Henricia sanguinolenta,* which had been maintained in an aquarium for 6 weeks, apparently without feeding, were placed in a fingerbowl containing a cloudy suspension of *Mytilus* sperm in sea-water, to which had been added a quantity of minute particles of Nile blue sulfate (sparingly soluble in sea-water). Externally, streams of particles could be observed converging upon the mouth, most rapidly and conspicuously in the ambulacral grooves. The mouths of both specimens remained open, much as in Figure 1, and while coarse clumps or large particles were rejected, smaller particles were either swept directly through the radial peristomial grooves at the angles of the mouth or entangled in strands or sheets of mucus which also moved into the stomach. After 12 hours' exposure to the suspension the animals were carefully washed to remove adherent particles and then dissected for examination of the digestive tract. In both specimens, concentrations of dye particles were found at various places in several of the Tiedemann's pouches.

Such a crude experiment should not be interpreted as having established the fact that in its normal nutrition *Henricia* is dependent upon a flagellary-mucous feeding mechanism or that this suffices for all its needs. The experiment does, however, provide a demonstration that at least under certain conditions particulate matter suspended in the surrounding water finds its way into the digestive tract. Further,

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[2] I take this opportunity of clearing up a misunderstanding involving functional relationships between the pyloric caeca and Tiedemann's pouches in *Patiria*. Irving (1926) performed digestion experiments with isolated surviving caeca of this species and concluded that these organs are capable of digesting gelatin and absorbing amino acids. Hyman (1955, p. 385) questions this interpretation on the ground that the pyloric caecum of *Patiria* ". . . is underlain on the oral side by an extensive stomach diverticulum (so-called Tiedemann's diverticulum . . .), so that in Irving's experiments the gelatin solution went into this stomach diverticulum and the resulting digestion is probably to be attributed to the stomach." It must be pointed out that in *Patiria* the cavity of the pouch is everywhere completely open to, and in free communication with, the median duct of the caecum, so that anything going into the one is very soon distributed and thoroughly mixed in all parts of the other. The stomach of *Patiria* contains a vanishingly small proportion of zymogen cells, and it has been experimentally established that digestion does not occur in the stomach of an animal that has been deprived of all its caecum-pouch complexes (Anderson, 1959). Zymogen cells do not occur in Tiedemann's pouches in *Patiria,* and the only apparent source of digestive enzymes in this species is in the epithelium of the pyloric caeca themselves. Therefore, while Hyman's criticism was certainly justified in the light of information then available, the facts that have subsequently been established make it clear that Irving's conclusions cannot properly be questioned for the reasons advanced by Hyman.

it shows that in the intact animal particles so ingested pass into the radial parts of the system by pathways previously deduced on anatomical and histological grounds and on the basis of experiments with excised organs. In the absence of any other information on food and feeding in *Henricia,* all the indirect evidence that can be brought to bear seems consistent with the conclusion that finely-divided particulate matter in suspension, exploited by a flagellary-mucous mechanism, is significant in the nutrition of this starfish. If this is valid, then the very close and detailed structural correspondence between the digestive system of *Henricia* and that of *Linckia,* particularly in relation to the highly specialized Tiedemann's pouches, makes it reasonable to extend this conclusion to *Linckia* also. I can find no information on the food or feeding habits of *Linckia guildingi.*

Flagellary-mucous feeding of the type suggested for *Henricia* (and *Linckia*) is not unknown among starfishes. The experiments and extensive observations of Gemmill (1915) on *Porania pulvillus* demonstrate that alone among the starfishes tested, individuals of this species are capable of maintaining themselves for long periods on a diet of suspended particles only. The external and internal currents by which this diet is manipulated are apparently similar to those described in *Henricia.* Gemmill makes no mention of Tiedemann's pouches in *Porania,* and I have been unable to determine from the literature whether they are present. The powerful currents produced by this starfish suggest the presence of some type of specialization of the general nature of the Tiedemann's pouches in *Henricia.*

Several species of starfishes known to be chiefly macrophagous have been suspected of utilizing particulate matter, also, to some extent. It is interesting that these same forms possess more or less well-developed Tiedemann's pouches. For example, Gemmill (1915) finds that flagellary currents carry considerable amounts of particulate food into the digestive tract of *Astropecten,* a sand-dwelling starfish well known as a voracious carnivore. The behavior of *Patiria miniata,* particularly with regard to its habitual exposure of the huge, everted cardiac stomach in the external environment (Anderson, 1959), strongly suggests that it may in this way collect significant amounts of particulate matter to add to its extremely varied diet. *Astropecten,* it will be recalled, has relatively small Tiedemann's pouches, while those of *Patiria* are much larger but of simple construction compared with the elaborate pouches of *Henricia* and *Linckia.* The significance of these structures may lie in the enhancement of circulatory efficiency which even small or simple pouches may contribute, in relation to feeding currents. The marked structural similarity between the digestive tract of *Patiria* and that of *Asterina gibbosa* (which according to MacBride, 1906, subsists principally upon sponges and ascidians) is strongly suggestive of extensive functional correspondences, perhaps including particulate feeding.

Resemblances involving visceral organs, and particularly those of the digestive tract, are usually considered less reliable as indices of taxonomic relationship than, for example, similarities in skeletal structures or other hard parts. Nevertheless, it is interesting to consider from this standpoint the fragmentary information available concerning the distribution of Tiedemann's pouches in starfishes. The similarities between the pouches of *Patiria* and those of *Asterina* are to be expected in genera belonging to the same family. Although the flagellary pumping organs of the *Patiria* type superficially resemble those of *Henricia* and both are called Tiede-

mann's pouches, they are fundamentally very different structures. The resemblances are so superficial, and the structural differences so profound, that one is led to conclude that in the Asterinidae and Echinasteridae these organs have evolved independently and convergently as solutions to the problem of increasing circulatory efficiency within the digestive tract. These two families, it may be noted, are by all accounts closely related members of the Order Spinulosa.

In contrast, Tiedemann's pouches and other features of the digestive tract in *Linckia* are astonishingly similar, at least in the material available to me for preliminary study, to those of *Henricia*. The similarities are so striking and extend to such details as to make it appear unlikely that they could have arisen convergently in unrelated lines of starfishes. Yet the Linckiidae, chiefly on the basis of skeletal features that are fundamental in asteroid taxonomy, are placed nowhere near the Echinasteridae but among the valvate Phanerozonia. However, MacBride (1906, p. 471) makes the following statement about the Linckiidae, interesting in the present context: "It is possible that these forms, so different in many respects from the other families of the order, may have been directly derived from the long-armed Echinasteridae." My observations on structural details of the digestive system seem strongly to support the idea of a closer relationship between these families than is indicated by the criteria commonly used in starfish systematics.

It is obvious that any attempt to survey similarities and differences in organ systems, and particularly to trace the distribution of anatomically and histologically specialized visceral structures, among the various families and orders of starfishes will be meaningless until it can be based upon vastly augmented data. These data accumulate slowly, requiring careful and detailed study of the internal anatomy of many species on which the literature to date offers only descriptions of external appearance, skeletal features, geographical distribution, and the like. The present attempt at a comparative study of Tiedemann's pouches in a small group of starfishes is inadequate, based as it is upon insufficient information. At least, however, it provides a tantalizing glimpse of the surprisingly broad areas of knowledge still awaiting exploration and interpretation in the Asteroidea.

Summary

1. Detailed study of the digestive system in *Henricia* reveals that as a result of regional differentiation, particularly involving the lining epithelium, areas specialized for zymogenic and mucous secretion are segregated from other areas adapted for current-production. Secretory areas include the five interradial pouches and vesicles of the cardiac stomach, the pyloric stomach generally but particularly its radial reservoirs, and the median ducts and lateral diverticula of the pyloric caeca. Current-producing areas include the five radial pouches of the cardiac stomach and the gutters leading upward to marginal openings low in the pyloric stomach, and especially the very elaborate Tiedemann's pouches which spring in pairs from these openings and extend along the oral midlines of the pyloric caeca. Other starfishes, such as *Asterias*, which lack Tiedemann's pouches, restrict their zymogen cells to the lateral diverticula of the caeca and crowd current-producing cells into the median caecal ducts, an area which in *Henricia* contains an extremely high concentration of zymogen cells.

2. Tiedemann's pouches in *Henricia* are divided into numerous parallel flagellated channels leading diagonally upward into the pyloric caeca. These channels are separated by unique partitions formed by adhesion-seams between opposite side-walls of the pouch. It is evident from their structure and anatomical relationships, and has been experimentally demonstrated, that Tiedemann's pouches are flagellary pumping organs of great effectiveness. They produce currents capable of drawing suspensions or solutions from the stomach and delivering them rapidly along almost the entire length of the pyloric caeca. Centripetal currents stream back into the stomach, and thus a constant circulation of materials can be maintained through the radial secretory and absorptive areas, depending chiefly upon currents generated in the close-set channels of the ten Tiedemann's pouches.

3. The customary food and the feeding habits of *Henricia* are unknown, but several lines of evidence, anatomical and experimental, combine to suggest that this starfish, like at least one other (*Porania*), may subsist either wholly or in part upon suspended particles gathered by a flagellary-mucous mechanism.

4. In *Patiria miniata,* a species not distantly related to *Henricia* (same order, different family), Tiedemann's pouches are present and lie in about the same relationship to the pyloric caeca but are fundamentally dissimilar; they lack separate flagellated channels, the side walls being traversed only by parallel stripes of mucous cells alternating with bands of typical cells, and thus are more bag-like in general structure. Although they function similarly to those of *Henricia,* these much simpler pouches are probably less effective in current production. *Asterina gibbosa,* closely related to *Patiria,* has *Patiria*-type Tiedemann's pouches. *Astropecten,* in which these pouches were originally described (1816), has relatively small ones of simple construction. Both *Patiria* and *Astropecten* have been suspected of supplementing their macrophagous diet by flagellary-mucous particle-feeding, and although their pouches are far less elaborate than those of *Henricia* they are probably of significance in this connection.

5. It is disconcerting to find that *Linckia,* not at all closely related to *Henricia* (different order), nevertheless has Tiedemann's pouches and other specializations of the digestive system similar in most respects to those of *Henricia.* The differences between the pouches in *Henricia* and *Patiria* are so fundamental as to suggest that they represent independently evolved solutions to the problem of increasing circulatory efficiency within the digestive tract. In contrast, the pouches of *Henricia* and *Linckia* resemble each other so strikingly that it is difficult to conceive of them as having been produced by convergent evolution.

6. It is pointed out that detailed studies on many species of starfishes now known only from external anatomy and skeletal features of preserved specimens will provide information upon which to base broader and more meaningful comparative surveys of internal specializations.

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